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The Effect of Human Predation on the Size Distribution of *Siphonaria gigas* (Mollusca: Pulmonata) on the Pacific Coast of Costa Rica

by

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Abstract. At a site accessible to fishermen, the mean and maximum sizes of *Siphonaria gigas* were smaller than at a National Park where limpets have remained undisturbed for at least 7 years. Measurements of empty shells and home scars of limpets that had been consumed by fishermen demonstrated a selection for larger limpets. At the site accessible to fishermen, the population of *S. gigas* has been kept at a reduced mean size. It has persisted because of the equilibrium between human predation and recruitment.

INTRODUCTION

MAN HAS COLLECTED shellfish for food since prehistoric times along rocky shores (SHIAPPACASSE & NIEMEYER, 1964; MONTANE, 1964; SPEED, 1969; PARKINGTON, 1977; DILLEHAY, 1984). Shell middens in South Africa date back 30,000 years (SPEED, 1969). In recent years the study of the disturbance by man on intertidal communities has become of primary importance especially in the Southern Hemisphere where human predation is intense (BRANCH, 1975; CASTILLA, 1981; MORENO *et al.,* 1984, 1986; CASTILLA & DURAN, 1985; SIEGFRIED *et al.,* in press; HOCKEY & BOSMAN, 1986; OLIVA & CASTILLA, in press). After the exclusion of man from biological reserves in Chile, the size distribution of some heavily harvested species changed drastically (MORENO *et al.,* 1986). Some of these species played a key role in the organization of intertidal communities (MORENO *et al.,* 1984; CASTILLA & DURÁN, 1985).

In this paper I document the effect of human consumption on the size distribution of the pulmonate limpet *Siphonaria gigas* Sowerby, 1825, on the Pacific coast of Costa Rica. *Siphonaria gigas* is one of the most abundant limpets along the Pacific coast of Central America (GARRITY & LEVINGS, 1983; LEVINGS & GARRITY, 1984; LUBCHENCO *et al.,* 1984; ORTEGA, 1985). It is predominantly found on exposed shores and returns to a home scar after each foraging excursion (GARRITY & LEVINGS, 1983). Although *S. gigas* can attain sizes of up to 80 mm in length in Panama (LEVINGS & GARRITY, 1984), the mean size in Costa Rica is usually smaller (ORTEGA, 1985, and this paper). I present evidence that suggests that humans, as size-selective predators, have reduced the mean size of *S. gigas* in areas accessible to them, whereas in areas protected from harvesting the mean size of *S. gigas* is larger.

STUDY SITES

This work was conducted at two sites along the Pacific coast of Costa Rica. The first site is the same as described in ORTEGA (1985), a rocky headland called Punta Mala (=Punta Judas) (9°31′N, 84°32′W). At this site, fishermen often visit the intertidal zone to fish and collect intertidal organisms for food. My observations were made on the extreme westerly point of Punta Mala (herein referred to as Punta Mala West). The second site, the southern point of a rocky shore at Manuel Antonio National Park, is located approximately 40 km south of Punta Mala. Collection of flora and fauna has been prohibited inside the park for 7 years. Both sites are exposed to moderate amounts of wave shock.

MATERIALS AND METHODS

To determine the mean size of resident populations of *Siphonaria gigas,* 9 and 10 permanent quadrats (0.25 m^2) were established in the mid-high intertidal zone (1.60–2.00 m above MLW) of Punta Mala West and Manuel Antonio National Park, respectively, in July 1984. Limpets were individually numbered with plastic tags glued to the shells with underwater polypoxy (Pettit Co., Spring

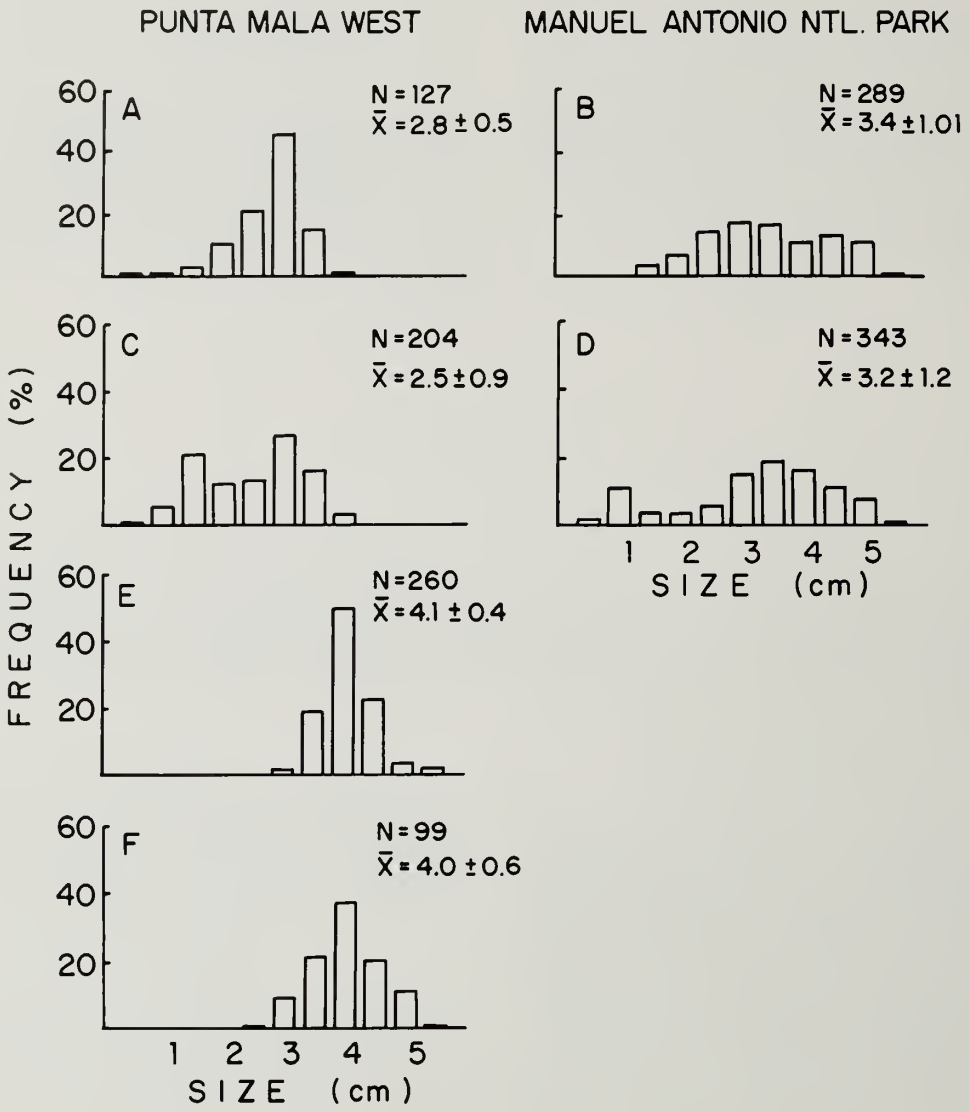

Figure 1

Size-frequency distribution of *Siphonaria gigas* at Punta Mala West (left column) and Manuel Antonio National Park (right column). A–D, resident populations; E, shell collection; F, shell midden. A and B July 1984; C–F November 1984.

Valley, CA). Shell length was measured to the nearest 0.1 mm with dividers (*e.g.,* SUTHERLAND, 1970) in July and November 1984.

To determine whether the difference in mean size of *Siphonaria gigas* between the two sites was due to a difference in growth rate, approximately 50 limpets (<2 cm in shell length) were individually numbered and the shell length measured at each site in November 1984. These limpets were measured again in February 1985. Only individuals labeled at both sampling dates were considered in the statistical analysis.

In November 1984 extremely low spring tides provided access to some isolated rock outcrops near Punta Mala West. Fishermen were observed collecting *Siphonaria gigas* at that time. On the following day, bits of limpet tissue were still present on some scars previously occupied by limpets. Because the shell margin of the limpet usually fits the rock exactly, the lengths of home scars were assumed to be equivalent to the lengths of limpets that had been collected. Empty scars as well as uncollected individuals were photographed at that time with a Nikonos camera using a 16 × 25-cm focal framer. Thirty six pictures were taken haphazardly for a total of 123 scars and 150 limpets. Lengths of empty scars and limpets were

Table 1

Mean size and length increase ± standard deviation (size ranges) of marked *Siphonaria gigas* at Punta Mala West (PMW) and Manuel Antonio National Park (MANP). Only numbered individuals (N) at both sampling times were included.

	n	November 1984	February 1985	Increase in length
PMW	33	1.6 ± 0.1 (1.3–2.0)	2.0 ± 0.2 (1.6–2.4)	0.4 ± 0.1 (0.2–0.6)
MANP	6	1.5 ± 0.2 (1.3–1.9)	1.9 ± 0.2 (1.6–2.1)	0.4 ± 0.1 (0.3–0.6)

measured from the photographs by projecting the negatives onto a computerized digitizing pad (Summagraphics bit pad, SUTHERLAND & ORTEGA, 1986).

Finally, shell lengths of *Siphonaria gigas* that had been collected by fishermen in November 1984 from the rock outcrop and from another site near Punta Mala West were measured. Shell lengths of *S. gigas* were measured from shells collected from a midden found near the house of a fisherman.

For simplicity, shell lengths were divided into size classes of 0.5 cm. Due to the heterogeneity of variances between samples, differences in mean size between sites were analyzed with a Kruskal-Wallis test (SOKAL & ROHLF, 1981).

RESULTS

The mean densities (number/m² ± SD) of *Siphonaria gigas* in the permanent quadrats at Punta Mala West were 56.4 ± 26.1 and 88.0 ± 60.0 for July and November 1984. At Manuel Antonio National Park mean densities for the same dates were 116.0 ± 33.6 and 110.8 ± 35.2 respectively.

The mean size of *Siphonaria gigas* at Punta Mala West in July 1984 was significantly smaller than at Manuel Antonio National Park (Figures 1A, B; Kruskal-Wallis test, $P < 0.05$, d.f. 1, $H = 36.61$). At Punta Mala West the maximum size of *S. gigas* was 4.1 cm whereas at Manuel Antonio National Park the maximum size was 5.5 cm. In November 1984 the mean size of *S. gigas* was again significantly larger at Manuel Antonio National Park (Figures 1C, D; Kruskal-Wallis test, $P < 0.05$, d.f. 1, $H = 70.62$). Maximum size of *S. gigas* was 4.2 at Punta Mala West and 5.5 at Manuel Antonio National Park. Smaller individuals (<1.5 cm) were more numerous in November than in July at both sites, suggesting that some recruitment had occurred during the period between samples.

Increases in length of juvenile limpets did not differ significantly between the two sites from November 1984 to February 1985 (Table 1; $P > 0.05$, d.f. 1,37, $F = 0.0030$) which suggests that the differences in mean and maximum sizes of limpets between sites were not due to differences in growth rate.

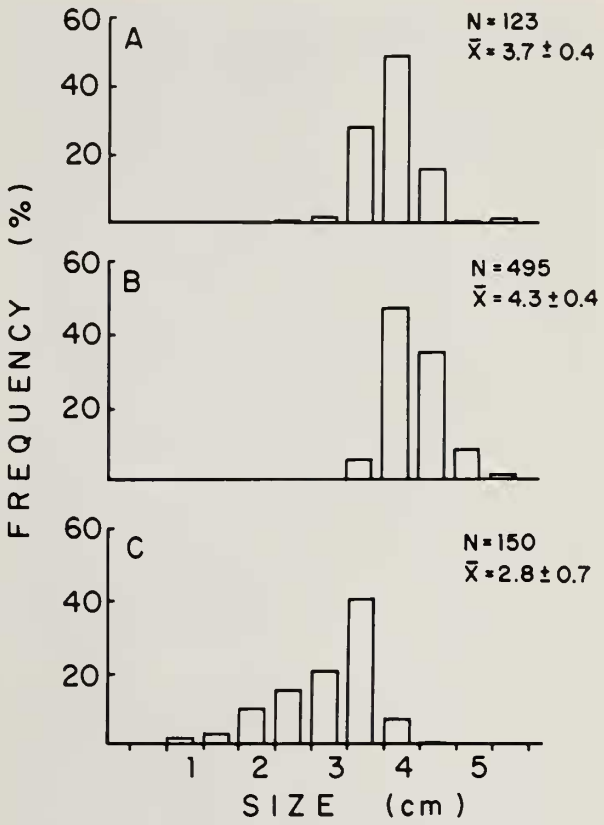

Figure 2

Size-frequency distribution of empty scar lengths (A), shell collection (B) and resident population (C) of *Siphonaria gigas* on an isolated rock at Punta Mala West in November 1984.

Measurements of shell collections from Punta Mala West indicated that the size range of limpets collected by fishermen was between 2.7 and 5.6 cm (Figures 1E, F, 2B). Large size classes were mostly absent in the resident population (Figures 1A, C). The size range of empty limpet scars was between 2.4 and 5.5 cm, which approximately coincided with the size range of the limpets collected by people from the same site (3.4 and 5.6; Figures 2A, B). The maximum size of the remaining population was 4.2 cm (Figure 2C) which was clearly smaller than the maximum size of empty scars and the shell collection. The larger size classes that were missing in the resident population were present in the size distribution of the empty scars, shell collections, and shell midden, which indicates a selection for larger limpets by human predators.

DISCUSSION

This paper demonstrates that human predation may play an important role in regulating the size structure of the

population of *Siphonaria gigas* on Punta Mala West. The mean size of *S. gigas* was smaller in the area visited by fishermen than in the National Park where collection was prohibited (Figure 1). Fishermen removed the larger sizes (Figures 1E, F, 2A, B) indicating that man is a size-selective predator (Branch, 1975; Moreno *et al.*, 1984, 1986; Hockey & Bosman, 1986). Selection for larger sizes has also been demonstrated for fish and thaid gastropods preying upon populations of *S. alternata* (Cook, 1980; Menge, 1973).

Homing behavior in limpets has been shown to be a defense against fish predation (Garrity & Levings, 1983; Frank, 1981). In Costa Rica, man, not fish, appears to be the main predator of limpets (Ortega, 1986). Neither a large size nor home scar provides a refuge from humans. Other limpets found at Punta Mala West, such as *Siphonaria maura* (Sowerby) and *Fissurella virescens* (Sowerby), are not eaten by man, the former because of its smaller size and the latter because of the widespread belief among local people that its unusual taste may be caused by a toxic substance. Many *Siphonaria* species are unpalatable or even toxic (Branch, 1981; Bennett *et al.*, 1983; Hockey, 1983; Branch & Cherry, 1985). Branch & Cherry (1985) demonstrated that *S. capensis* produces a milky mucus when irritated. This limpet is avoided by fish, birds, and seastars that commonly feed on other limpets. Bigalke (1973) reported that indigenous people on the southern African coast harvest patellid limpets but not siphonariids in spite of their abundance and accessibility. *Siphonaria gigas* is the only *Siphonaria* species in which polypropionates (presumed to be antipredatory chemicals) have not been detected (Faulkner, personal communication). Clearly *S. gigas* has no antipredatory defenses against humans.

Along the Pacific coast of Costa Rica *Siphonaria gigas* reaches larger sizes in areas inaccessible to fishermen than in areas disturbed by them. Intense predation might drive a species to local extinction. This appears to have occurred at Punta Mala West for the coiled gastropod *Nerita scabricosta*. *Siphonaria gigas* has persisted at Punta Mala West because intense recruitment (Ortega, unpublished data) has balanced predation by man.

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